Territory and feeding in the stickleback (Gasterosteus Aculeatus) a test of the resident/intruder effect

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TERRITORY AND FEEDING IN THE STICKLEBACK

(GASTEROSTEUS ACULEATUS)

A TEST OF THE RESIDENT/INTRUDER EFFECT

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" Much has been said and written in the past few years to create a taste for the aquarium and the crawling, cold-blooded inhabitants of the water. There was quite a mania for awhile to make an acquaintance with the stickleback and the newt, and every one was professing an interest in the gyrations of a goggling gulping carp or the mountebank antics of a lively minnow! Well! Chacun à son goût - everyone to his taste as the French say. "

The Rev. Francis Smith : The Canary, Its varieties, breeding and management. 1878.

ACKNOWLEDGEMENTS

I would like to thank Dr. N. Dunstone for supplying me with much of the experimental equipment - tanks, partitions, the experimental cell, sticklebacks and the like.

My special thanks are due to my supervisor Dr. P.J.Greenwood, who provided the idea for the project. His constructive criticisms, especially in the writing-up stages were extremely helpful.

CONTENTS

CHAPTER ONE

INTRODUCTION

A territory can be defined as an area occupied more or less exclusively by an animal or group of animals by means of repulsion through overt defence or advertisement (Noble 1939, J.L.Brown 1964 Wilson 1971b). Territories have been described for a wide variety of animals, both vertebrates and invertebrates (Brown & Orians 1970, Wilson 1975).

A territory can be defended by an animal for a number of reasons one of which is access to food supply. It can be argued that individuals which occupy an area more or less exclusively are able to obtain information regarding the food in that area. Davies & Houston (1981) and Kamil (1978) looked at the feeding behaviour with respect to territory of Pied Wagtails (*Motacilla alba*) and Hawaiian Honeycreepers (*Loxops virens*). Both these studies found that intruders into territories obtained on average, less food because they did not know where recently depleted areas of territory were located. Tresspassing was unprofitable. They suggest that an advantage of territory ownership was that the birds knew where the food supply was abundant and as a result had a high feeding rate. However it is also possible that an unfamiliar location per se (regardless of a lack of knowledge of food supply) may cause a reduction in feeding. This is because, in an alien territory an animal may have to be on the look out for predators and/or the territory owner and therefore not be able to devote as much time to feeding. This study attempts to investigate these two ideas using a relatively simple predator/prey interaction which includes a territorial component.

The predator chosen was the three-spined stickleback (Gasterosteus aculeatus), a convenient species for a number fo reasons. It can be regarded as a typical territorial species. The territorial behaviour patterns are most fully developed in the adult males; there is a clearly delimited area within which the males of the same species begin to display to intruders, especially other adult males; the resident male usually wins any disputes and the elaborate posturings adopted by the males are bluffs - serious injury or death is a rare outcome.

In shallow ponds and rivers during spring and early summer male three-spined sticklebacks defend nest sites against other conspecific males. The territory is the area surrounding the nest site within which the aggressive posturing displays documented by Tinbergen (1953) take place. Alongside such activities as courting females, chasing off intruding males and care of the nest site, the male has to feed. Sticklebacks in the wild will take a wide range of aquatic invertebrates, water fleas, Daphnia spp. are frequently eaten.

Sticklebacks defend territories to attract females. (Van der Assem 1967). This has given rise to a wealth of literature concerning courtship behaviour and territorial defence. However, little attention has been given to the feeding behaviour of sticklebacks with respect to territory.

Milinsky (1977a &1977b) studied the feeding behavoiur of three-spined sticklebacks upon a simulated swarm of Daphnia. They attacked an experimental cell divided into several compartments filled with varying numbers of Daphnia. The fish bit at this 'swarm' and the regions attacked could be noted. Moreover, because the prey were not depleted the reaction of a fish to a swarm of constant numbers over a period of time could be gained.

Milinski and Heller(1978) found that a predator influenced the feeding behaviour of three-spined sticklebacks. A behaviour pattern such as feeding should be the result of optimisation processes involving costs and benefits to the animals fitness.

However a feeding strategy which is 'optimal' in one situation may not prove to be so when other pressures such as predation are apparent. Milinski & Heller (1978) found that the presence of an avian predator (a black silhouette of a European kingfisher Alcedo atthis 16cm beak to tail length) altered the feeding strategy of the three-spined stickleback upon a simulated swarm of Daphnia. Before exposure to the kingfisher model - when the predation pressure on the fish is low, the fish directs its attacks at areas of high prey density. With decreasing attack readiness, for example as induced by decreasing hunger they show a preference for less dense regions and direct the last attacks at stragglers. However, after exposure to the model of the kingfisher the sticklebacks feeding behaviour changes and the swarm regions of low density are attacked. These areas of the swarm provide a lower feeding rate but it is suggested increase the ability of the fish to detect a predator. This is due to the so-called 'confusion effect' arising from the highly bunched Daphnia at the centre of the swarm.

Allen (1920) describes the attacks of a loon (Garia immer Brunnich) upon a shoal of sardines (Sardinella coeruleus). He notes that the bird made numerous dashes at the shoal but each time came up without apparently catching any fish. He suggests the possibility that 'The bird was unable to make a choice amongst so many chances before the opportunity was gone.' Miller (1922) in discussing the significance of flocking in animals states that 'in the lower animals the confusion arising from divided attention is much greater than in ourselves....division of attention means failure.'

Consider the case of a male stickleback which has entered into another fish's territory and is feeding upon a Daphnia swarm. It will be experiencing a 'stress' not unlike that induced by the avian predator, except that in this case it is caused by the presence of the owner of the territory. In this thesis I suggest and test the hypothesis that in an alien territory the stickleback experiences divided attention;should it attack the dense region of the swarm where a confusion effect may impair its ability to detect the approach of the resident male. Therefore the stickleback may change its feeding behaviour under such circumstances and attack the less dense regions of the swarm where the confusion effect is also less.

By attacking the region of low prey density (in the experiments to be described this is the periphery of the swarm) the stickleback incures a cost, namely the lower rate of energy intake but this is offset by the benefit of being able to detect the approach of the resident male and take evasive action if neccessary. As such this could be interpreted as an optimal foraging strategy.

However, as already stated removal to a new locality per se could be responsible for a change in feeding. A novel environment may on its own induce a stress which may alter feeding rates. If this is so, intuitively one would assume that food intake would be reduced and I test this hypothesis in Chapter 3.

Also sex differences may exist in the feeding behaviour of the stickleback. Males in breeding condition could be less motivated to feed at a high rate. A territorial male has several other activities to perform as well as feeding such as attracting females to the nest site and chasing off other males; these could effectively lower its overall feeding rate and again intuitively, this seems to be a reasonable hypothesis.

Therefore any change in the feeding behaviour of a stickleback in the territory of another fish could be due to:-

1) The presence of the territory owner.

2) The new locality or

3) Dependent upon the sex and/or motivational state of the fish.

It seems likely that any feeding behaviour so observed will probably be multicausal but I have attempted in the experiments ~~to~~ which follow to separate these three causal factors and so obtain an estimate of the importance of each.

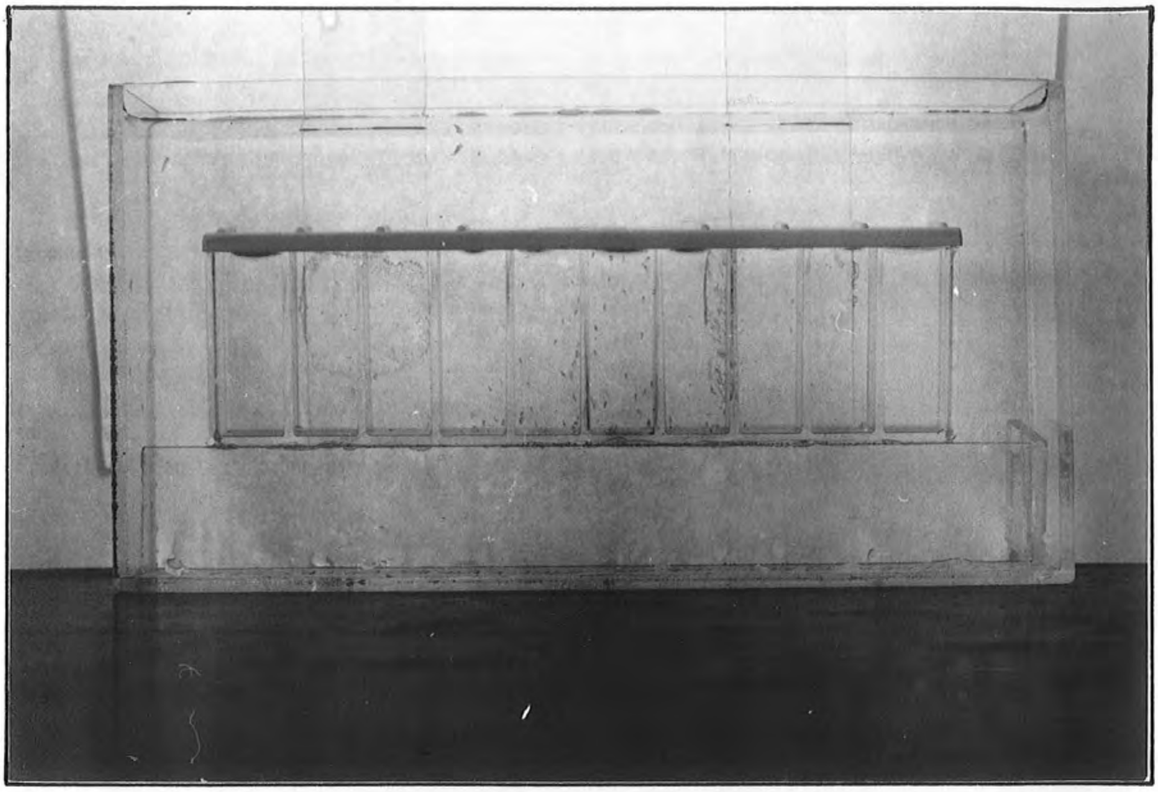


PLATE 1 : THE EXPERIMENTAL CELL

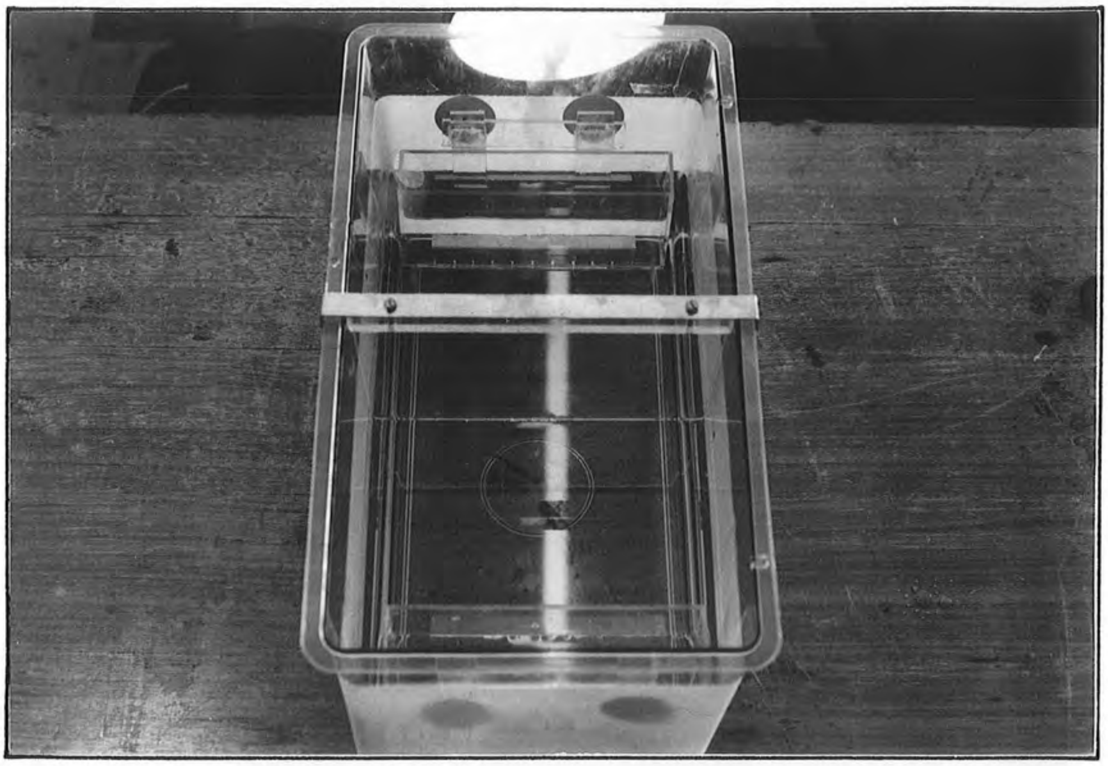


PLATE 2 : EXPERIMENT 4 : TWO MALES DISPLAYING TO EACH OTHER ACROSS THE CLEAR PARTITION.

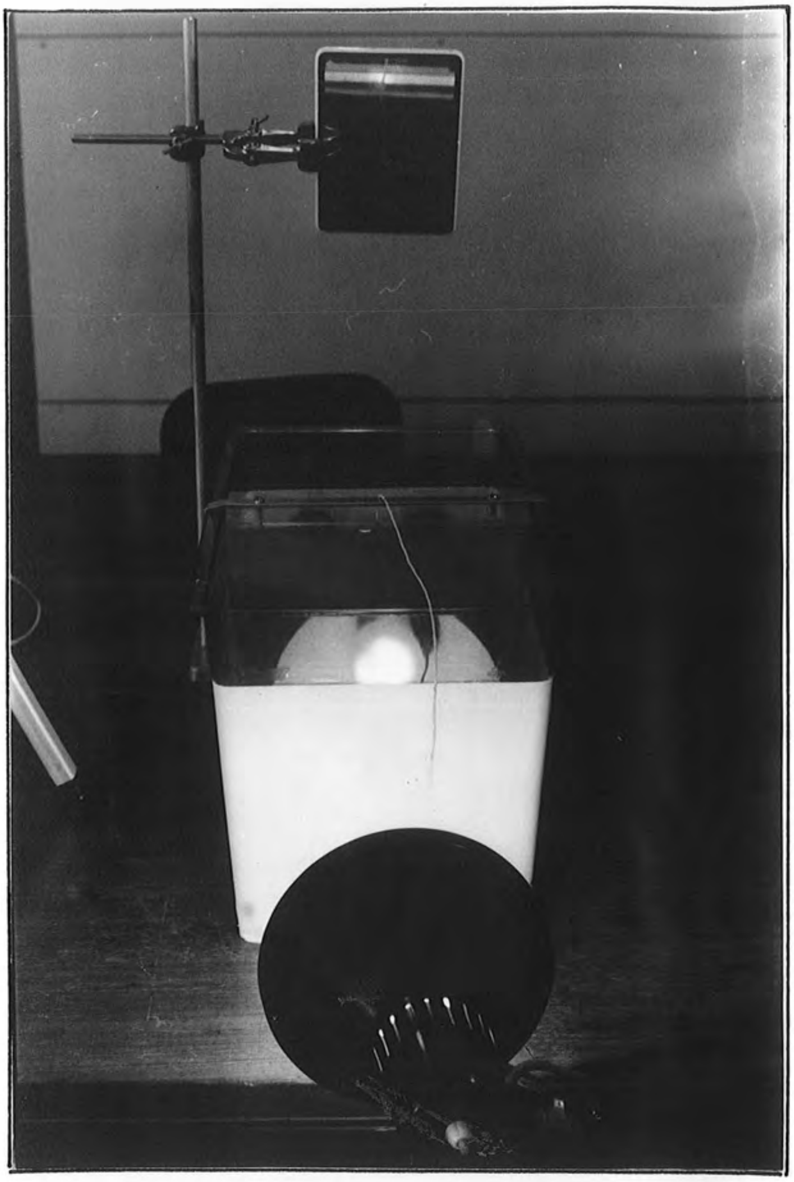


PLATE 3 : EXPERIMENTAL SET UP FOR EXPERIMENTS 1 2 & 3.

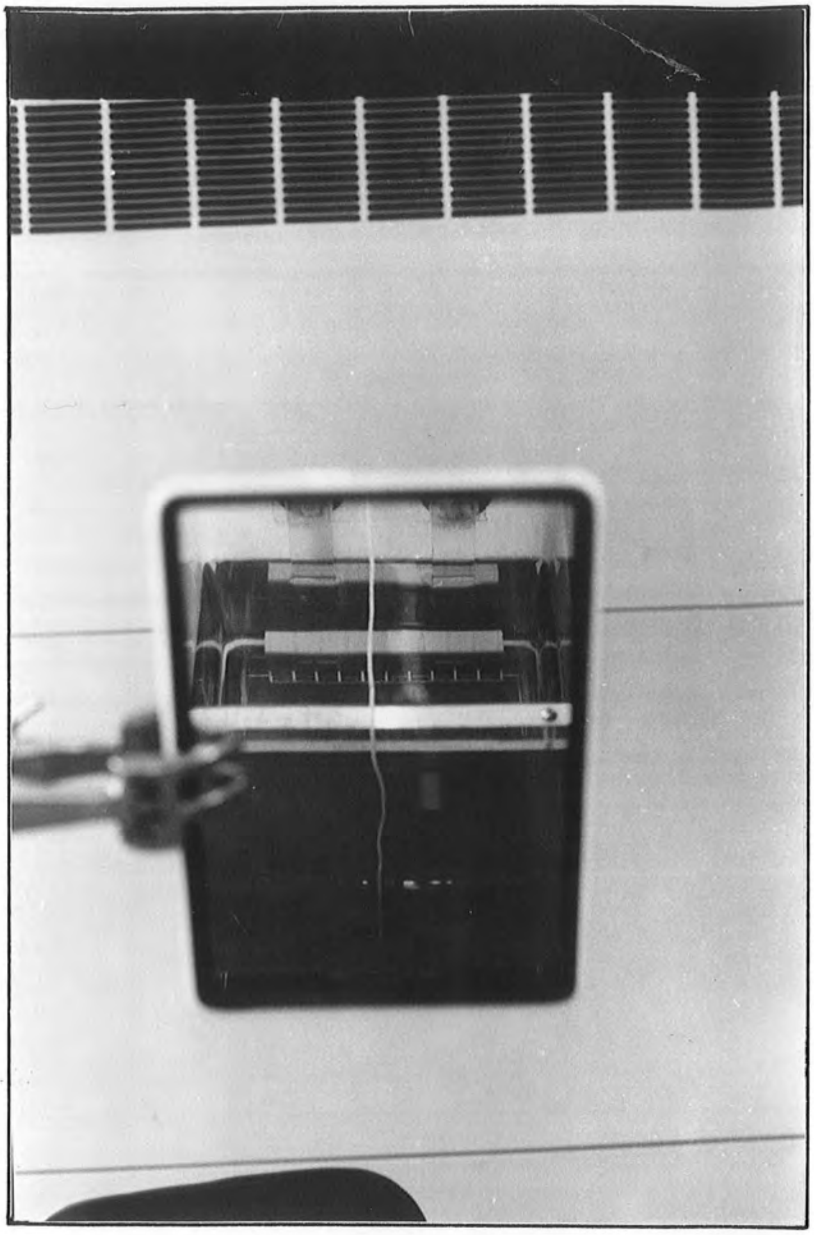


PLATE 4 : OBSERVERS VIEW OF THE EXPERIMENT IN THE MIRROR

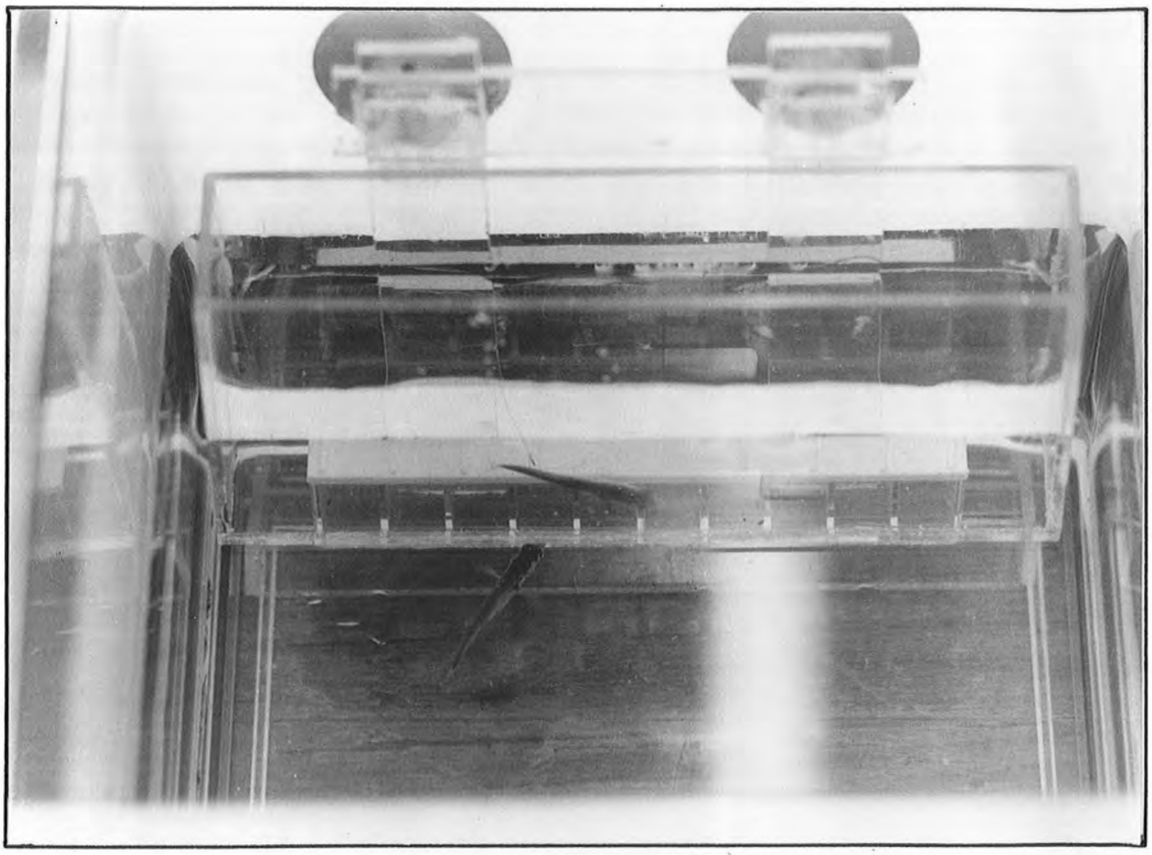


PLATE 5 : EXPERIMENT 4 : A MALE ATTACKING THE EXPERIMENTAL CELL BELOW THE CONFINED MALE

CHAPTER TWO

METHODS

The basic experimental set up follows fairly closely that described by Milinsky and Heller (1978). All experiments were carried out under laboratory conditions in a 15°C constant temperature room under a light regime of 16 hours daylight and eight hours darkness during May, June and July 1981. The particular light regime was chosen in order to simulate a long daylength thus ensuring that the males remained in reproductive condition and exhibited territorial behaviour.

The experimental cell containing the *Daphnia* differed slightly from that used by Milinski and Heller. It consisted of ten chambers each of base 1cm x 1cm and 3cm high and was constructed in 1mm thick transparent plastic. The cell was suspended 2cm off the base of the tank by two vertical perspex struts attached to the top wall of the tank by two rubber suckers. An additional strut of perspex ran along the bottom of the cell, touching the base of the tank in order to prevent the fish from swimming up and underneath the cell. The top of the experimental cell was detachable enabling the ten chambers to be filled up with the required number of *Daphnia*.

Care was taken to ensure that the *Daphnia* used in the experiment were of equal size, measuring around 1.5mm total body length (excluding tail spine). Individuals with large numbers of parthenogenic offspring or eggs were avoided as these may have been more obvious to the fish than other individuals. After five consequetive experiments the Daphnia were mixed between the cells.

For all experiments 30 Daphnia were placed in the middle two cells ten in the adjacent two, then five, then one, then zero, (see Plate 1). This arrangement was chosen in order to mimic as closely as possible the appearance of a natural swarm of Daphnia in the water. The individual cells were completely filled with water, the detachable lid slid across the top and the whole assembly submerged in the experimental tank.

All the fish were adult individuals of the three-spined stickleback (Gasterosteus aculeatus) and were obtained from two sites: the Experimental Field Station pond, Durham University and the pond at Van Mildert College, South Road, Durham. Batches of fish were collected throughout May, June and July but were kept for at least a week before testing in the experimental tank. The males were confined singly in tanks measuring 30cm x 20cm x 20cm whereas the females were kept together in a large aerated tank. The females were somewhat larger that the males (females mean length 4.3 cms, males 3.9 cms.) but mean fish length did not differ significantly between experiments. Whilst in captivity the fish were fed on a diet of blowfly maggots and pupae supplemented by dried fish food on which they appeared to thrive. Some losses were incured, mainly due to outbreaks of white spot disease, but such losses were at an acceptable level of below 5% overall. All fish tested in the experiments were (visibly) healthy.

The plastic experimental tank measured 40 x 25 x 20 centimetres and the walls were covered on the outside with white paper in order to produce diffuse lighting. The water level in the tanks was kept at 12cm. Illumination was provided by two 2.5 metre long strip lights on the ceiling about a metre to the left and right of the tank. In addition the experimental cell was further lit to make sure that the Daphnia were readily visible to the sticklebacks by a 60W angle poise lamp situated 15cm away from the back wall of the tank (see Plate 3). The experimental cell could be observed by means of a mirror held on a retort stand placed at the opposite end of the tank from the cell and angled slightly downwards. This enabled the observer sitting some two metres away from the tank to view the fish without disturbance. Plate 4 shows the observers view of the experiment in the mirror (see also Figure 1).

EXPERIMENTS 1 2 & 3 (SEE CHAPTER 3)

A grey perspex partition was placed vertically in the centre of the tank in the base of which was a trap door measuring 2.5 x 3cms. (Milinski & Heller 1978) which could be raised and closed at will by the observer using an attached length of string. (see Figure 2 and Plate 3). The experimental cell containing 0 1 5 10 30 30 10 5 1 and 0 Daphnia in its ten compartments was attached to one inside wall of the tank whilst on the other side of the partition an empty but otherwise identical cell was placed.

Each stickleback was starved of food for 24 hours prior to testing. The fish under test was carefully introduced into the side of the tank containing the empty cell with the trap door in the down position To ensure that the fish reacted to the cell four Daphnia were placed in the tank along with the fish and not until these had been consumed was the trap door lifted. The fish was then free to swim through into the other side of the tank and attack the experimental cell. Once through the trap door was closed.

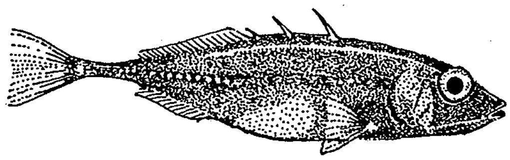
EXPERIMENTS 4 5 6 & 7 (SEE CHAPTER 4)

The grey perspex partition was replaced by a clear partition of equal size through which a fish on one side of the tank could see and display to another. An experimental cell was placed in each half of the tank, one containing *Daphnia*, one empty as before and a stickleback introduced on either side of the partition. An hour later it was assumed that the two fish were aware of each others presence on either side of the tank and the fish not being tested (on the side containing the experimental cell) was placed in a container of dimensions 19 x 4 x 10cm constructed of 3mm clear perspex mounted so that its base of 19 x 4cm rested on top of the experimental cell. With the stickleback successfully confined the partition was gently and smoothly removed by hand to avoid frightening the fish which swam through and attacked the experimental cell below the container holding the confined stickleback.

DATA RECORDING

In all experiments bites were recorded using a hand held tape recorder. The number of *Daphnia* in the cell being attacked was spoken into the microphone. The first bite was noted at zero seconds and timing was continued until a bite had not been noted for 120 seconds. This could be done whilst watching the reaction in the mirror (see Figure 3). The tapes were played back and transcribed using a stop watch; the time and position of each particular bite was noted on the data sheets. The observer recorded a bite when the fish made a direct run at and contact with the cell, characterised by a downward motion of the snout (see Figure 4). This was often followed by a rapid backing off.

In experiments 4,5,6,&7 the number of and time of attacks at the confined individual was also noted. An attack was regarded as a definate run at the container and was usually followed by a bite at the confined fish. Twenty individuals were tested in each experiment.



X2

<u>FIGURE 1</u> : THE PREDATOR : <u>GASTEROSTEUS ACULEATUS</u> THE THREE-SPINED STICKLEBACK.

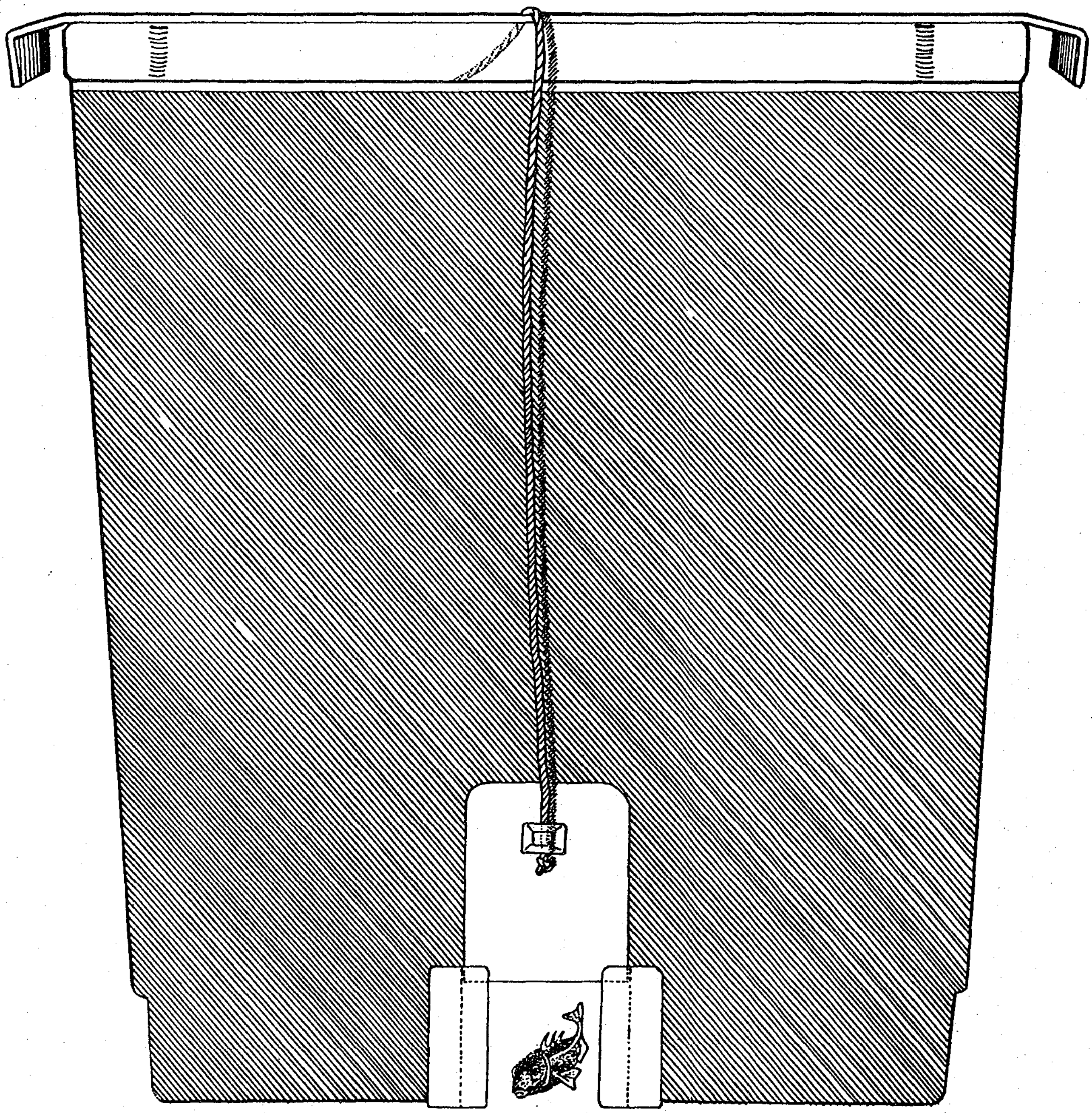


FIGURE 2 : THE GREY PARTITION USED IN EXPERIMENTS 1 2 & 3 WITH THE TRAP DOOR IN THE UP POSITION.

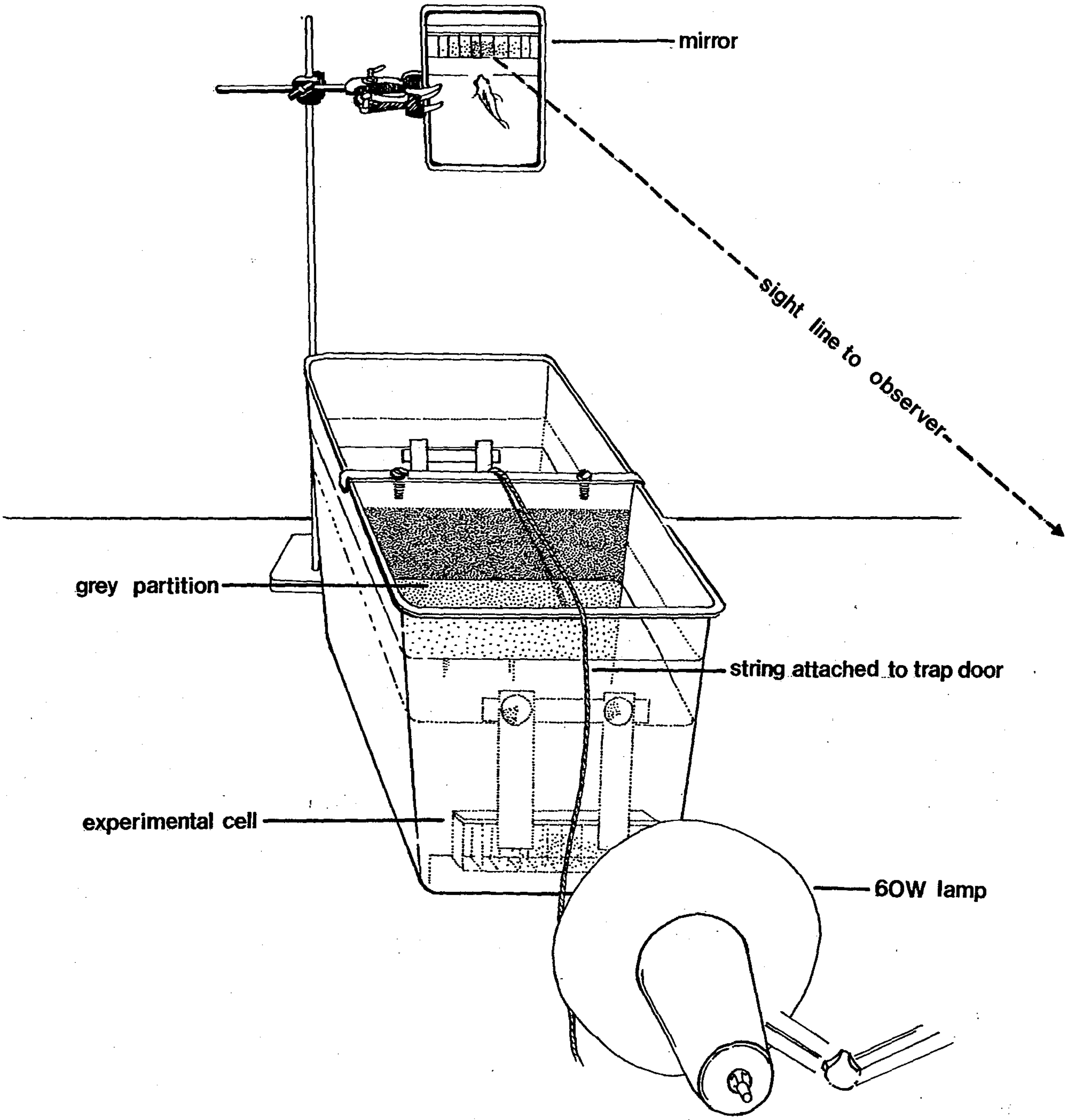


FIGURE 3 : EXPERIMENTAL SET - UP USED IN EXPERIMENTS 1 2 & 3.

SEE ALSO PLATE 3.

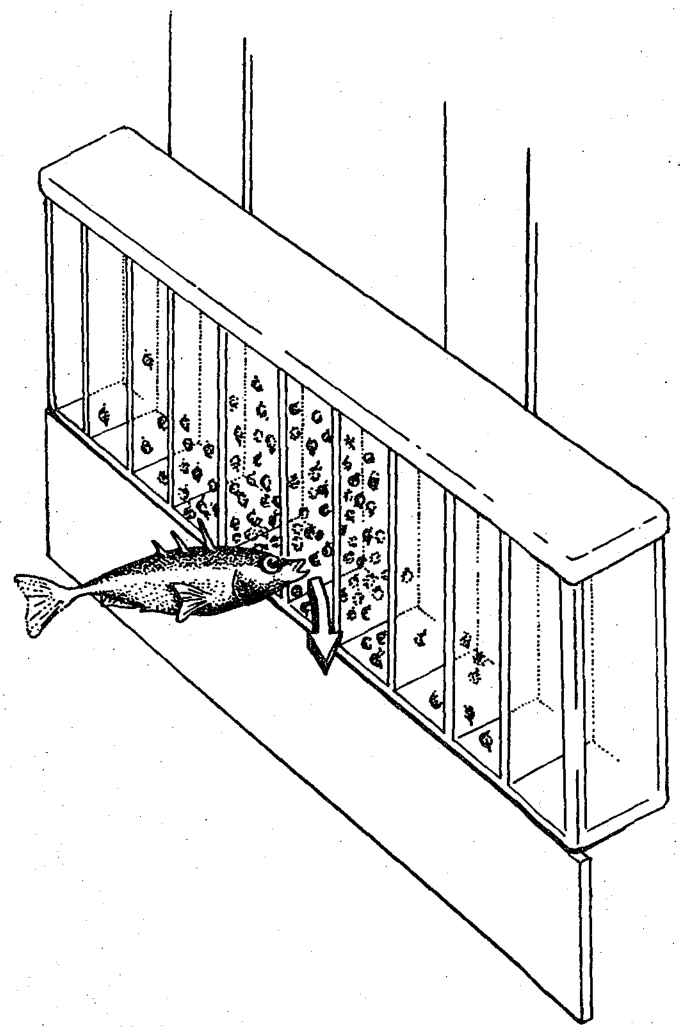


FIGURE 4 : STICKLEBACK ATTACKING THE EXPERIMENTAL CELL
A BITE IS CHARACTERISED BY A DOWNWARD MOTION OF THE SNOUT. NOTE THE RAISED SPINES.

FIGURES 5 - 11 : Bite frequency results (Experiments 1 - 7).

A = First bite position

B = First ten bites per fish (mean)

C = All bites per fish (mean)

n = Total bites scored by 20 fish.

The break in the histogram C represents half of the total number of bites scored.

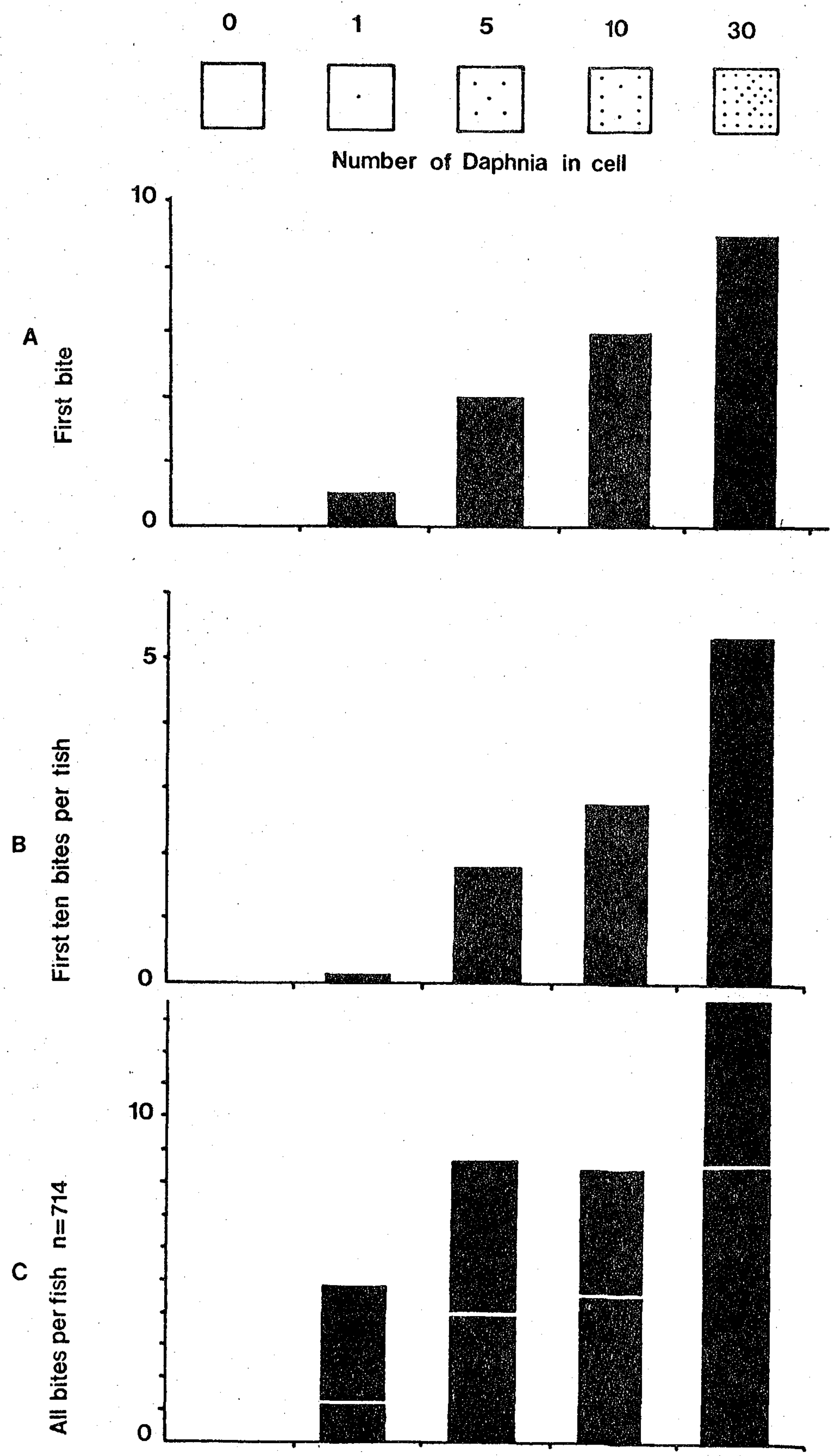


FIGURE 5 : EXPERIMENT 1. FEMALES

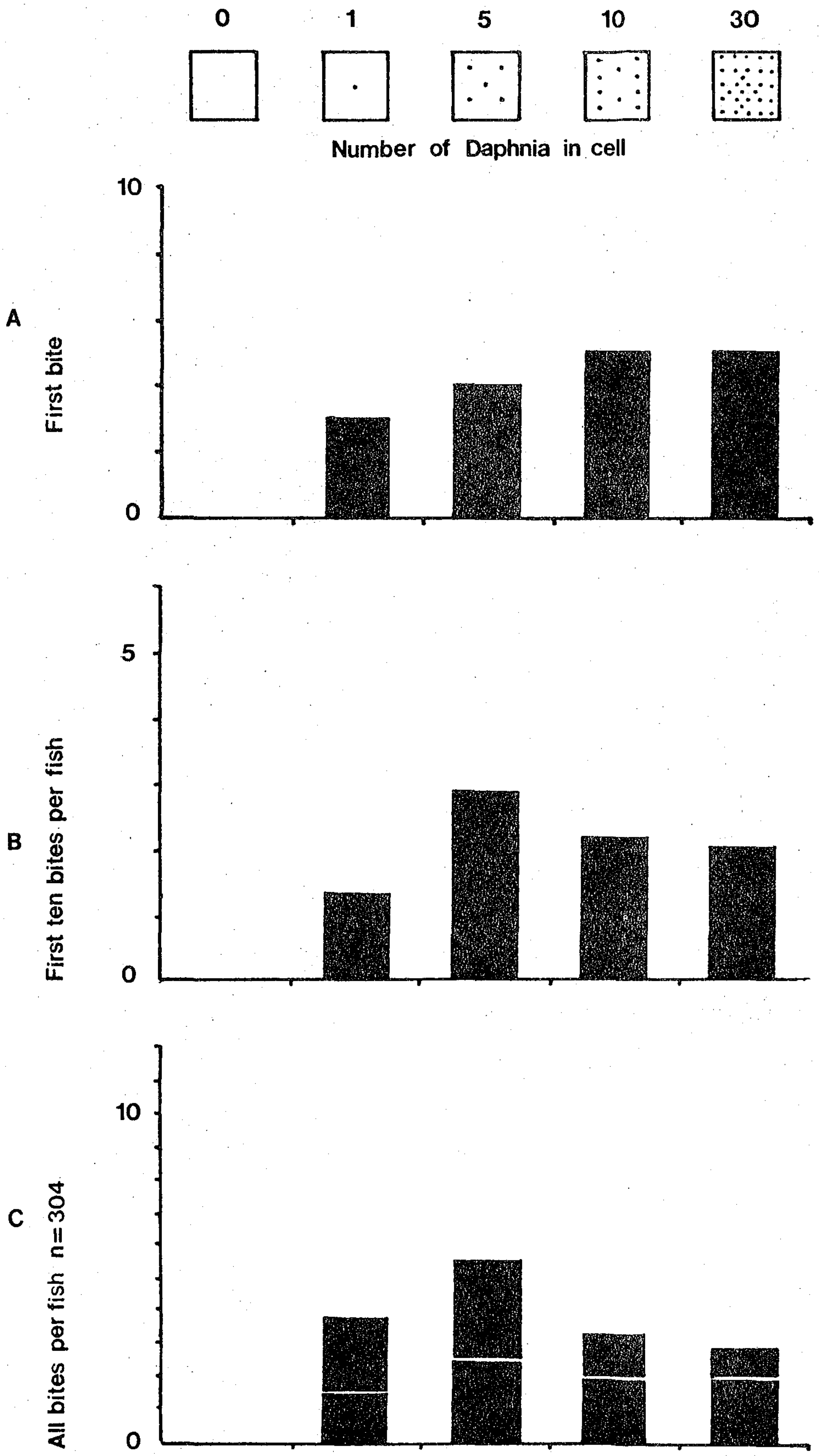


FIGURE 6 : EXPERIMENT 2. MALES

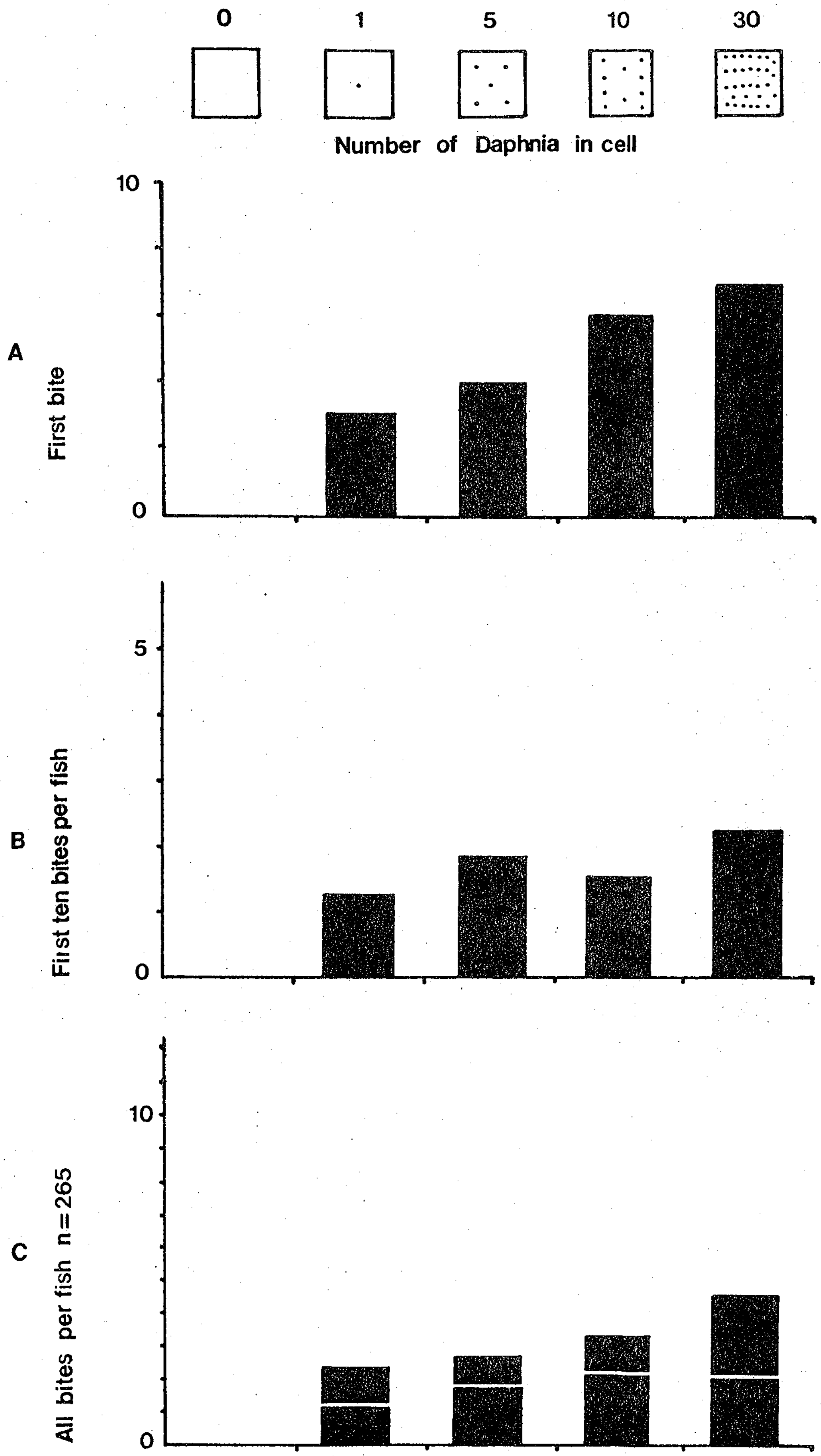


FIGURE 7 : EXPERIMENT 3. MALES OWN TANK

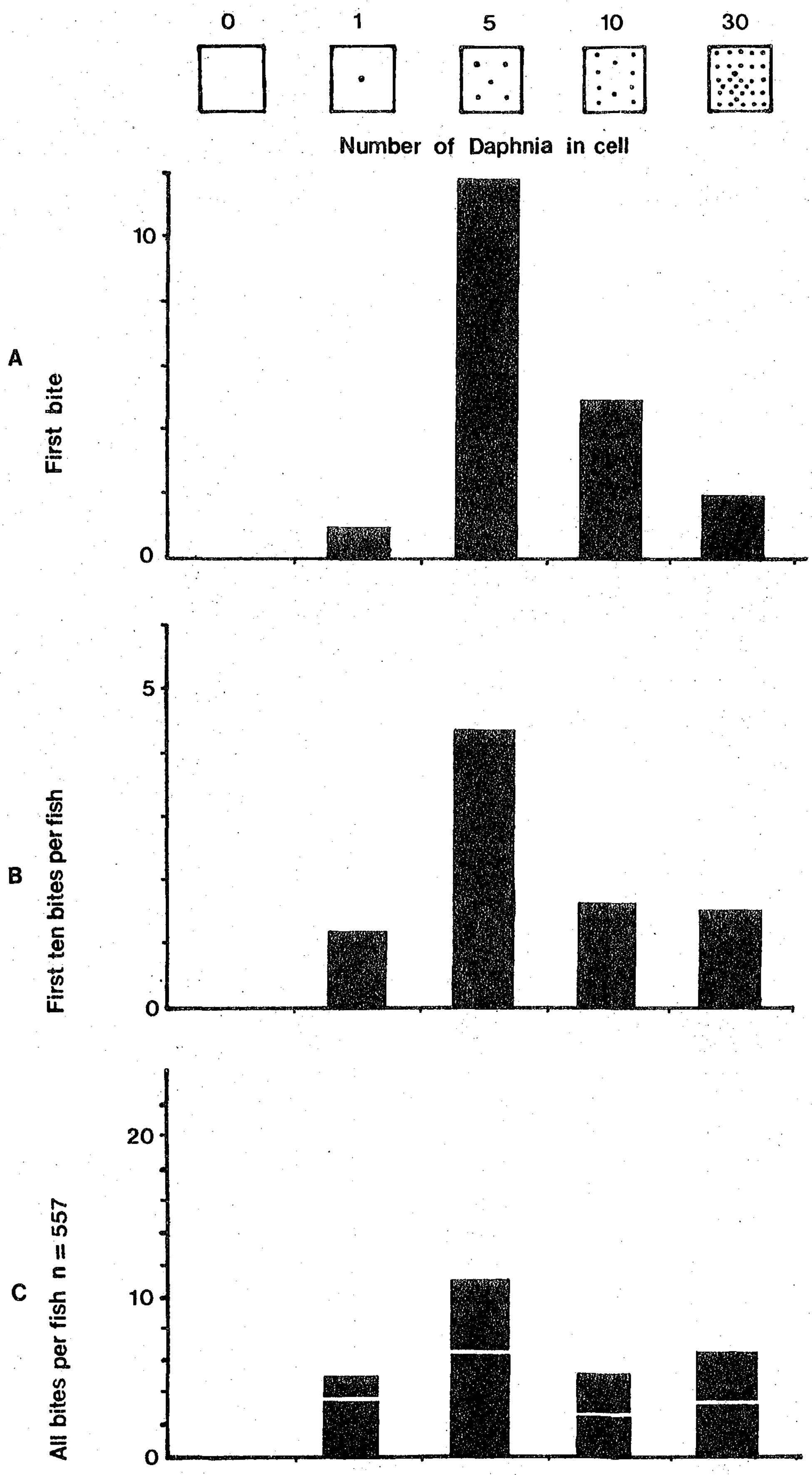


FIGURE 8 : EXPERIMENT 4. MALES : MALES

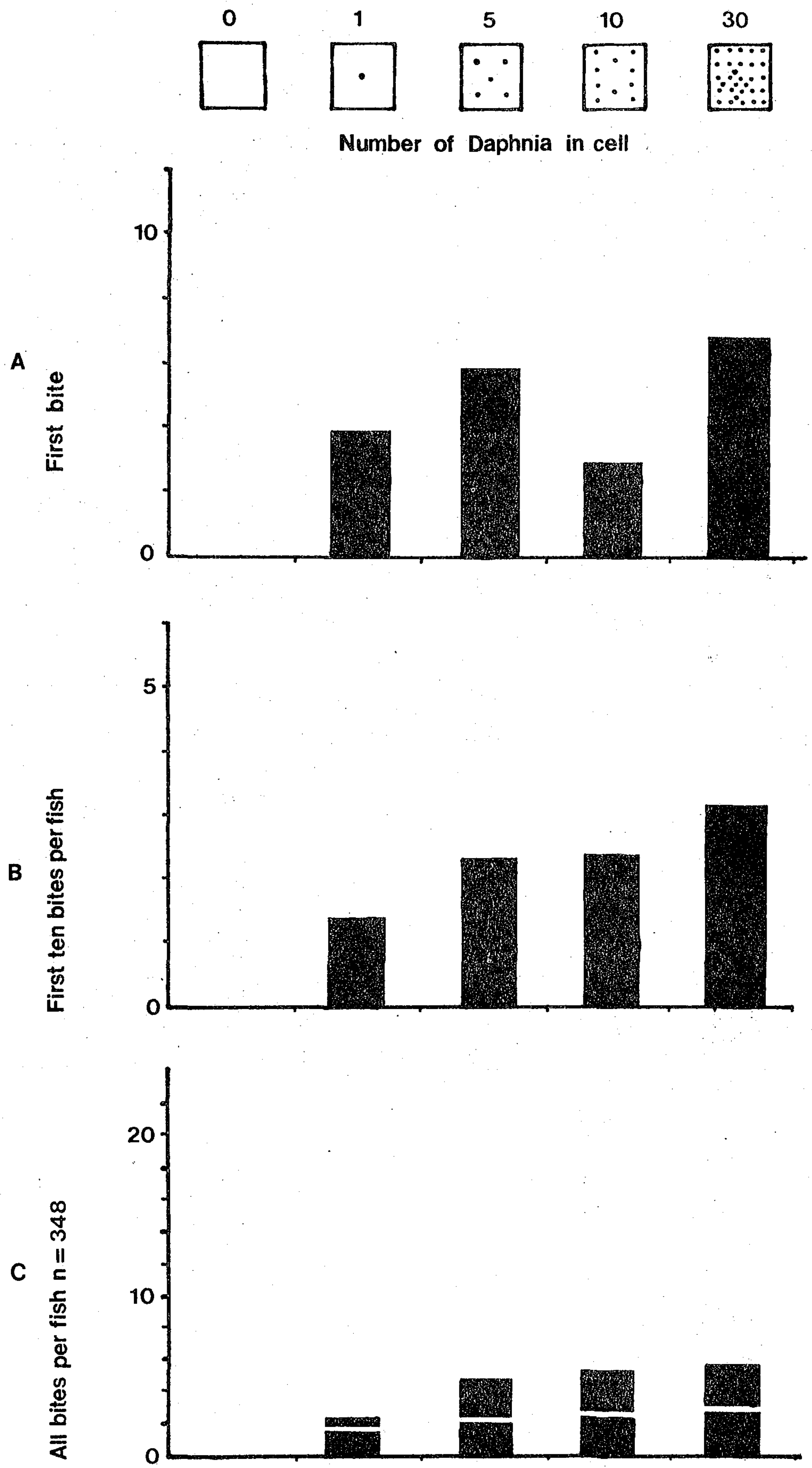


FIGURE 9 : EXPERIMENT 5. MALES : FEMALES

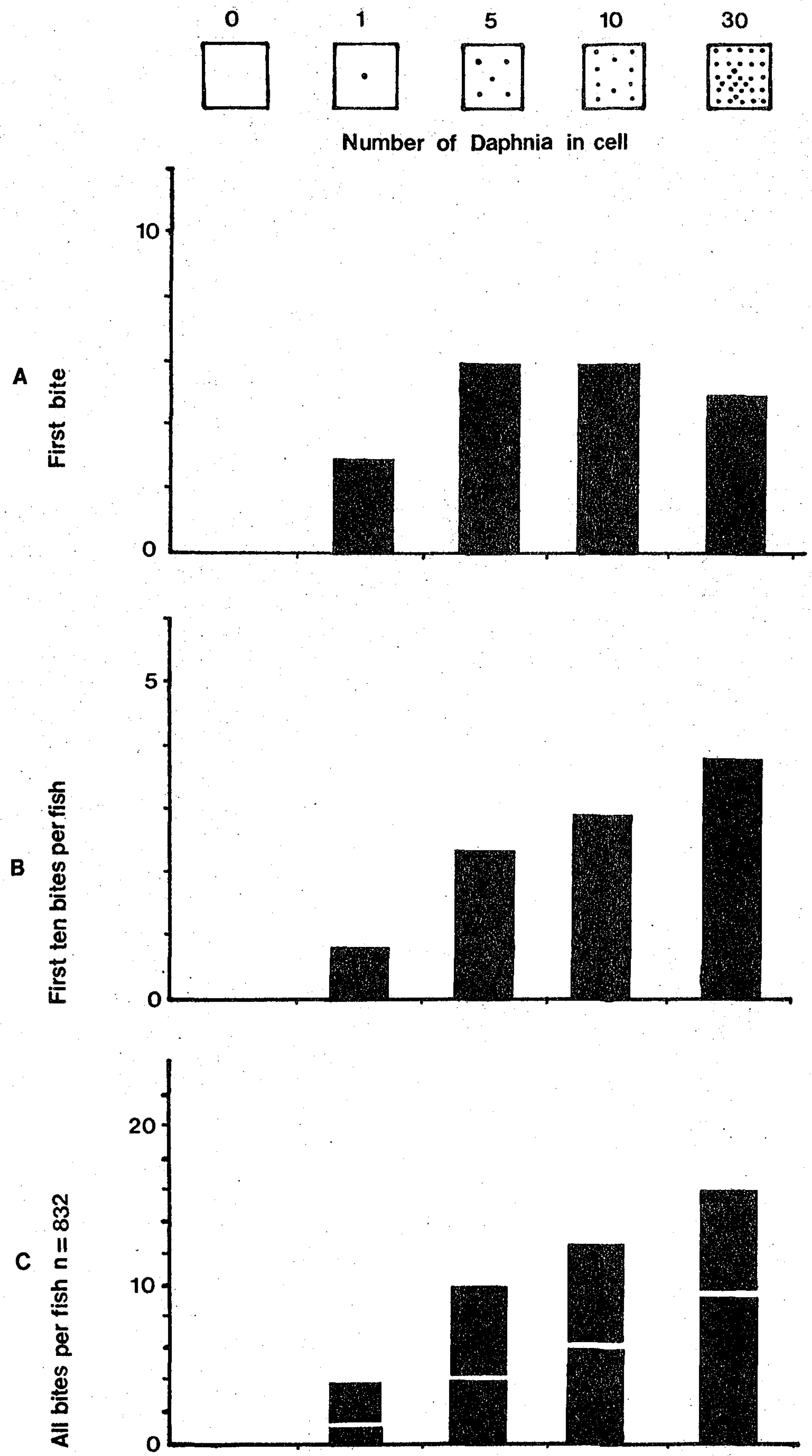


FIGURE 10 : EXPERIMENT 6. FEMALES : MALES

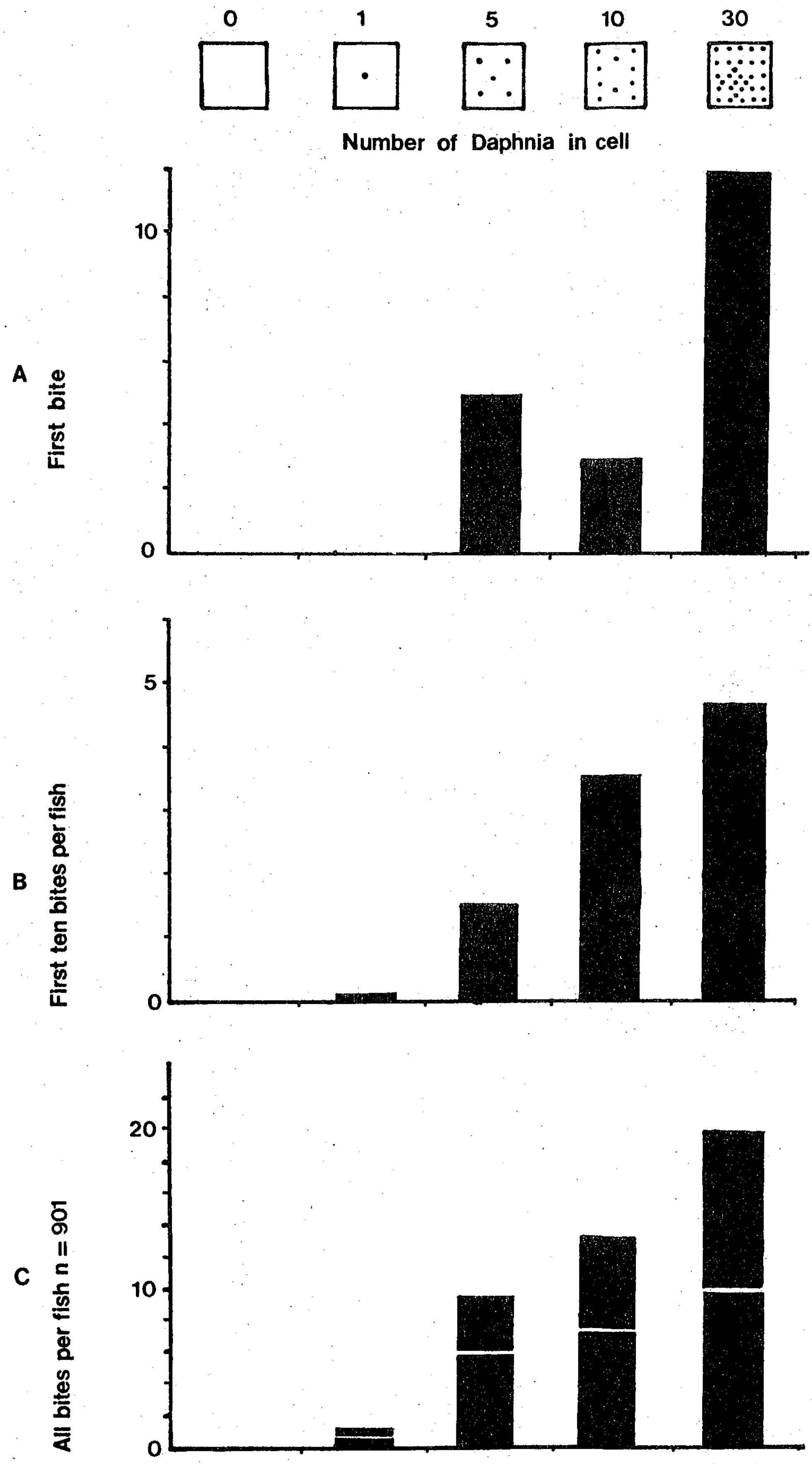


FIGURE 11 : EXPERIMENT 7. FEMALES : FEMALES

CHAPTER THREE

A) SEX DIFFERENCES IN ATTACK

Milinski (1977a & 1977b) studied the feeding behaviour of three-spined sticklebacks upon a simulated Daphnia swarm under laboratory conditions. He found that the area of the swarm attacked depended upon the attack readiness or motivational state of the fish. For example hungry fish preferred individuals at the centre of the swarm, sated fish preferred less dense regions.

Other factors than hunger could also affect the motivational state of the fish. Male sticklebacks in breeding condition may show differences in feeding behaviour to females. This could be due to the fact that a male fish spends a great deal of its time defending the nest site from intruders, (especially other males) and attracting females. Therefore the male may be less motivated to feed and if this is so we can expect a difference in the feeding rates of males and females.

The above hypothesis was investigated in the following manner. Twenty males and twenty females were tested in the experimental tank described in the previous chapter. After eating the four Daphnia they all passed through the trap door within ten minutes and reacted to the experimental cell. The mean reaction times from the trap door to the first bite were for females 8.95 seconds and for males 6.44 seconds. Males appeared to be more wary and were easier to scare with a sudden movement over the tank than females. After passing through the trap door the fish normally halted about 10cms away from the cell for a moment before attacking an area of the swarm. Feeding took place in bouts, both the number of bouts and bites within a bout decreasing with time (more than half of the total bites overall were made in the first half of the feeding time). Overall females made significantly more bites than males (Mann-Whitney $U=46.5$ $p<.002$). The results were also analysed in order to detect differences in the region of the swarm attacked by males and females. See Table 1 below :-

POSITION OF BITES	U VALUE	SIGNIFICANCE LEVEL
1	164	not significant
5	135	$p < .1$
10	82	p .002
30	73	p .002

TABLE 1 : Mann-Whitney analysis of Experiment 1 and Experiment 2. ($n_1=20$ $n_2=20$)

From Table 1 we can see that Females make significantly more bites at the centre of the Daphnia than males ($p < .002$).

B) CHANGES IN LOCALITY

We can now ask, does removal to a new (unfamiliar) locality cause a change in the number and/or feeding position in male sticklebacks. Between the experiments the male sticklebacks were confined singly in tanks of similar dimensions to the experimental tank. They were carefully transferred into the experimental tank and left alone for a couple of minutes to settle down. Males appeared to be more disturbed by this than females and on three occasions a male fish spent some fifteen minutes swimming up and down the walls of the tank. These fish were discarded. Four Daphnia were introduced into the tank and once eaten the trap door was opened (see Chapter 2)

In order to test the effect of this movement to a new locality upon males, the male fish were also tested in their own tanks which could be considered as familiar territory. Any differences in feeding behaviour between these two conditions could be interpreted as due to the new locality (the experimental tank).

EXPERIMENT 3

An empty experimental cell was introduced into the males tanks and after 24 hours it was replaced with a cell containing the Daphnia swarm with great care. The bites scored on the cell were recorded in the usual manner. The results were tested against experiment 2 to see if removal to a new locality causes a change in feeding. (see Figures 5 & 6).

The total number of bites recorded was not significantly different from experiment 2 (Mann-Whitney U=169.5). Table 2 shows analysis of the bite position. There appears to be little, if any difference in the areas of the swarm attacked in the two instances - (though males in the experiment 2 show a slight tendency towards attacking the cell containing 5 Daphnia - Mann-Whitney U=136.5 $p < .1$)

Therefore we can conclude that there is little evidence that removal to a new locality on its own causes a change in feeding in male sticklebacks. The U value of 136.5 is too high for the analysis to show a meaningful change in locality effect.

POSITION OF BITES	U VALUE	SIGNIFICANCE LEVEL
1	170	not significant
5	136.5	$p < .1$
10	153.0	not significant
30	156.0	not significant

TABLE 2 : Mann-Whitney analysis of Experiment 2 and Experiment 3. (n =20 n =20)

We have seen that there is a clear sex difference in the feeding behaviour of male and female sticklebacks. Females concentrate their attacks on the centre of the swarm (the tendency diminishing with time see Figure 4C) - whilst males show a bias towards the outer edge of the swarm. There does however appear to be no effect due to a new locality per se in males.

If the new locality is owned by another male we may expect to see a change in the feeding behaviour of any male intruding into that territory. The presence of a male stickleback above the experimental cell may distract the attention of the male under test. It seems possible that due to the confusion effect discussed in Chapter 1, the male may switch its attack to the outside of the Daphnia swarm. This hypothesis is tested in the next chapter.

CHAPTER FOUR

THE RESIDENT/INTRUDER EFFECT

Milinski and Heller (1978) found that sticklebacks change their feeding behaviour when a predator is present (a model of a kingfisher *Alcedo atthis*). Instead of concentrating their attacts at the centre of the *Daphnia* swarm they bite at the outside where it was argued, the confusion effect is less, enabling the fish to detect the predator with greater ease.

The same may be true for a stickleback feeding in an alien territory, for here the ability to detect the approach and possible attack of the resident male will be at a premium. I tested this using the experimental set up described in chapter 2. The stickleback under test was allowed to attack the experimental cell whilst a second fish was confined in a transparent perspex container above the cell. In this way the effect of the presence of another fish upon the individual under test could be investigated.

Experiment 4 involved 20 male sticklebacks - each fish's reaction was noted when another male was confined above the experimental cell. In addition to attacking the experimental cell all the males launched attacks directly at the confined male. Some attacks were very persistent. The mean time length of an attack upon the confined male was 4.45 seconds and the fish made an average of 17.5 attacks. The results of Experiment 2 were compared with those of Experiment 4. Table 3 over leaf shows the result of Mann-Whitney analysis of the bite position.

POSITION OF BITES	U VALUE	SIGNIFICANCE LEVEL
1	151	not significant
5	122	$p < .05$
10	156	not significant
30	220	not significant

TABLE 3 : Mann-Whitney analysis of Experiment 2 and Experiment 4. ($n_1 = 20$ $n_2 = 20$)

Males feeding in a tank in the presence of another male make significantly more bites at the cells containing 5 Daphnia than males feeding without a male (Mann-Whitney $U=122$ $p < .05$). Therefore it seems that the presence of a male above the experimental cell initiates a change in feeding behaviour on the part of the male under test.

Experiment 5 tested the reaction of a male to the experimental cell in the presence of a female. Under these conditions the male did not show the bias towards the outside of the swarm as in Experiment 4. (Compare Figures 8 & 9).

Experiments 4 & 5 are compared below:-

POSITION OF BITES	U VALUE	SIGNIFICANCE LEVEL
1	103	$p < .02$
5	99	$p < .02$
10	179	not significant
30	175	not significant

TABLE 4 : Mann-Whitney analysis of Experiment 4 and Experiment 5. ($n_1 = 20$ $n_2 = 20$)

Males make significantly more bites at the outside of the swarm when another male is present than when a female is confined above the cell. This suggests that a male stickleback does not consider a female to be a threat, yet the presence of another male is sufficient to divert its attacks towards the edge of the swarm.

Experiments 6 and 7 involved a female feeding in the presence of a male and in the presence of another female. (see Figures 10 & 11). Table 5 overleaf examines the results of these two experiments with female sticklebacks with Experiments 1 and 2. This analysis shows that females feeding in the presence of a male show no significant difference from females feeding on their own. Not suprisingly perhaps, in view of the sex difference in feeding behaviour shown in chapter 3a, females feeding plus a male make more bites at the centre of the swarm than do males feeding on their own. The same is true for females feeding plus another female. Comparison of the bite position data for Experiments 6 and 7 show that when a male is present, a female will make more bites at the cell containing single Daphnia (Mann-Whitney $U=92$ $p<.02$). This suggests that females consider males more of a potential threat than other females, if we assume that the confusion effect and the feeding changes described in previous chapters applies to females as well as males.

BITE NUMBER

Males feeding in the presence of another male make significantly more bites overall than the males tested in experiment 2 (on their own) (Mann-Whitney $U=106$ $p<.002$). It appears that the presence of another male stimulates the male to increase its bite rate. However

	POSITION OF BITES	U VALUE	SIGNIFICANCE LEVEL
Experiment 6	1	191	not significant
Experiment 1	5	186	not significant
n =20 n =20	10	169	not significant
	30	182	not significant
Experiment 6	1	166	not significant
Experiment 2	5	110	$p < .02$
n =20 n =20	10	72	$p < .002$
	30	67	$p < .002$
Experiment 6	1	92	$p < .02$
Experiment 7	5	200	not significant
n =20 n =20	10	168	not significant
	30	175	not significant
Experiment 7	1	194	not significant
Experiment 1	5	182	not significant
n =20 n =20	10	123	$p < .05$
	30	128	$p < .1$
Experiment 7	1	154	not significant
Experiment 2	5	117	$p < .05$
n =20 n =20	10	29	$p < .002$
	30	17	$p < .002$

TABLE 5 : Mann-Whitney analysis of Experiments 1, 2, 6 & 7. See text for explanation.

this is not the case when a female is present (experiment 5). (Mann-Whitney $U=197.5$ not significant).

The feeding behaviour of male sticklebacks clearly seems to change when it feeds in the presence of another male. More bites are made towards the outside of the swarm. This may be due to the confusion effect already described. The next chapter takes this idea further by attempting to find more evidence of this effect.

CHAPTER FIVE

BITE PATTERN

In Chapter 4 the resident/intruder effect was investigated. Male sticklebacks feeding in the presence of another male make significantly more attacks at the periphery of the swarm of *Daphnia* than when either the male is absent or a female is present in the container above the experimental cell. From this we can infer that the male regards the other male as a threat and modifies its behaviour to take this into account. The fact that males make on average 17.5 attacks at the confined male per reaction but only an average of 2.75 attacks at a confined female, suggests that this may indeed be the case.

The results obtained in Experiments 4 and 5 can be further analysed to attempt to find further evidence of the resident/intruder effect. The tendency to change cells; that is shift its attack from one region of the *Daphnia* swarm to another may suggest that a stickleback is experiencing a 'stress' due to the presence of the male confined above the experimental cell. Blackbirds (*Turdus merula*) feeding in alien territories (where the risk of being ousted by the resident bird is high), tend to shift their feeding areas, seldom concentrating on any one area for long (P.J.Greenwood pers comm.) By moving around from one feeding area to another the birds can increase their looking up rate - enabling them to detect the approach of the resident bird. The environment can be scanned more efficiently and it is possible that the same tactic may 'work' for the stickleback. Therefore the number of changes of cell within a feeding bout were looked at.

A) <u>CHANGES OF CELL</u>

The behaviour of a stickleback attacking the experimental cell containing the swarm of *Daphnia* followed a reasonably constant pattern. The feeding bout consisted of a series of consecutive bites at a cell, followed by a change to another cell and so on. There appeared to be a greater number of consecutive bites in the first half of the reaction time, in particular the first few bites all tended to be directed at the same cell.

The number of changes of cell were investigated in the data from Experiments 1 and 2 in order to find out if under the same conditions, male sticklebacks will change cells significantly more often than will females.

Assuming a linear relationship between the number of changes within a feeding bout (x) and the number of bites (y), a value Z was computed for each of the 20 trials in the experiment where:-

$$Z = \frac{y - \bar{y}}{x - \bar{x}}$$

$\bar{x}$ = mean number of changes in the 20 feeding bouts.

$\bar{y}$ = mean bite number in the 20 feeding bouts.

The Z values (n_1=20 n_2=20) were then compared using the Mann-Whitney.

When the results of Experiment 1 are compared with those of Experiment 2 a U value of 189 is obtained (not significant). Therefore under the same experimental conditions there is no evidence that male sticklebacks change cells more often than females.

We can now ask, does the presence of a male in the container above the experimental cell, rather than a female, cause an increase in the number of changes of cells. In simple language, are male sticklebacks more 'jumpy' in the presence of another male than in the presence of a female.

The data from experiments 4 and 5 was analysed as above and it was found that in terms of the tendency to change cells, a male stickleback behaves in the same manner as a female in the presence of another male. (Mann-Whitney U=162 not significant).

B) CONSECUTIVE BITES

Another way of looking at this problem is to see if there is any change in the number of consecutive bites made on a cell with different experimental conditions. A straight comparison of the number of consecutive bites between males and females could be misleading for in all the experiments females make more bites than males and therefore they may also appear to make more consecutive bites. In order to avoid such spurious results the following transformation was performed on the data:-

$$X = \frac{\text{Number of consecutive bites per cell}}{\text{Total number of bites made upon that cell}}$$

X is a measure of the tendency for a fish to make consecutive bites. If X = 0.5 then half or the bites scored were followed by a bite on the same cell. The X values were compared for Experiments 1 and 2. (See Table 6 overleaf). The results show that females make significantly more consecutive bites at the central four cells than do males.

POSITION OF BITES	U VALUE	SIGNIFICANCE LEVEL
1	183	not significant
5	170	not significant
10	119	$p < .02$
30	77	$p < .002$

TABLE 6 : Mann-Whitney analysis of Experiment 1 and Experiment 2. ($n_1 = 20$ $n_2 = 20$)

Males feeding in the presence of another male (Experiment 4) are no less likely to make consecutive bites than females feeding in the presence of a male (Experiment 5). See Table 7 below.

POSITION OF BITES	U VALUE	SIGNIFICANCE LEVEL
1	162	not significant
5	188	not significant
10	140	not significant
30	163	not isgnificant

TABLE 7 : Mann-Whitney analysis of Experiment 4 and Experiment 5 ($n_1 = 20$ $n_2 = 20$)

The same result was obtained when the X values of Experiment 4 and Experiment 2 were compared. The presence of another male does not appear to change the likelihood of a male making consecutive bites. Table 8 overleaf shows the U values generated by the Mann-Whitney analysis of these results.

POSITION OF BITES	U VALUE	SIGNIFICANCE LEVEL
1	176	not significant
5	190	not significant
10	192	not significant
30	178	not significant

TABLE 8 : Mann-Whitney analysis of Experiment 4 and Experiment 2. (n_1=20 n_2=20)

Female sticklebacks make significantly more consecutive bites than male sticklebacks under the same conditions. However the analysis did not show up any other differences either in the tendency to change cells or make consecutive bites between the various experiments. Therefore no real supportive evidence has been provided for the resident/intruder effect discussed in previous chapters. It may be that the observed shift in the area of the swarm attacked which we see when males feed in the presence of another male is sufficient on its own to enable the fish to raise its level of vigilance without a need for increasing the number of changes of cell. Attacking the periphery of the swarm may be enough. A fish which makes a large number of changes may suffer a drop in feeding rate. The male which attacks the outside of the swarm due to the presence of another male is already lowering its feeding rate - a further drop due to cell switching may not be necessary if the level of vigilance is high enough by attacking the outside alone.

CHAPTER SIX

DISCUSSION

Many species of animals defend territories. Male three-spined sticklebacks defend areas around the nest site from which other conspecific males are excluded. Previous studies of territorial behaviour have tended to focus on the aggressive posturing displays characterising territories; little attention has been given to feeding with respect to territories.

The experimental system used tests the importance of several factors which may cause differences in the feeding behaviour of sticklebacks under laboratory conditions.

MOTIVATION

In the breeding season males may not be motivated to feed at as high a rate as females. Males are more likely to be motivated towards activities such as courting females and care of the nest site. Male sticklebacks defend territories to attract females. Females however need to maintain a high feeding rate in order to satisfy the demands of egg production; a high feeding rate is at a premium for females. Rohwer (1978) notes that females but not males can be caught in the breeding months with just a worm tiéd to a piece of string.

Good evidence was found for such a sex difference in feeding behaviour. In all experiments females made significantly more bites than males and differences were discovered in the area of the *Daphnia* swarm attacked. Females preferred the centre of the swarm. An interesting finding was that a male feeding in the presence of another male (Experiment 4) scored significantly more bites than a male feeding on its own <u>or</u> a male feeding in the presence of a female. It seems that the presence of the confined male in Experiment 4 stimulates the males under test to feed at a higher rate. It is difficult to construct a reasonable hypothesis to explain this, one can only speculate that perhaps the male feeding in the presence of another male increases its bite rate in an 'attempt' to obtain as much food as possible before being ousted by the other male. This idea assumes that the resident/intruder effect is in operation and the male under test considers the confined male to be a threat (see later in this discussion).

CHANGE OF LOCALITY

The possibility that removal to a new locality could perhaps, on its own induce a change in the feeding behaviour of male sticklebacks was investigated. However, the results did not support such an idea. Both the area of the swarm attacked and the number of bites recorded remained unaffected by locality. Male sticklebacks were more susceptible to disturbance when moved into the experimental tank than females - three males made no attacks at the experimental cell at all. This could be due to the lower motivation to feed in male sticklebacks discussed above and so the evidence for a locality effect remains at best, slight. Also it is possible that a locality effect could be operating but hidden due to the resident/intruder effect in experiment 4. Clearly more work is needed to separate these factors.

CONSPECIFIC EFFECT

The third idea tested was that the presence of a male stickleback (which can be regarded as the territory owner or resident) can influence the feeding behaviour of an intruding fish. Previous studies of feeding behaviour suggest that an intruder obtains a lower feeding rate because it is unaware of the whereabouts or nature of the food supply in that area. The resident/intruder effect suggests that there is an extra dimension to this problem. Intruding males show quantitative and qualitative changes in their feeding behaviour. This is probably due to the need for vigilance - the approach and possible attack of the resident must be detected. The results support such an idea - male sticklebacks preferentially attack the outside areas of the *Daphnia* swarm when another male is present (Experiment 4). I have argued that this is due to a confusion effect which may impair the fish's ability to detect the presence of a territory holding fish should it attack the dense centre of the swarm; the peripheral regions are therefore preferred. The switch to the outside of the swarm which occurs when there is a male present does not occur when a female is present. This suggests that males only regard other males as a threat and so change their feeding behaviour accordingly. Females are 'ignored'.

It is important that the results of such experiments are applicable in the natural environment of the animals under study. Obviously the question must be asked, do sticklebacks show the observed behaviour patterns in the wild? Unfortunately, due to time constraints in the study there was no opportunity to investigate the problem under field conditions. Some studies of territory and feeding have been carried out on other animals however. Davies and Houston (1981) looked at the winter territories of Pied Wagtails (Motacilla alba) and discovered that territory ownership enabled a bird to achieve a higher feeding due to its ability to calculate return times for the renewable resource (dead flies washed up on stream banks) within its territory. Intruders did not achieve such a high feeding rate because they were unaware of the state of the food supply and were more likely to feed in recently depleted areas than were residents. Kamil (1978) found similar results in a study of Hawaiian honeycreepers (Loxops virens). Zach and Falls (1976b) noted that territory owning ovenbirds tended to avoid recently depleted areas of their territory. They stated '....since a territorial system enabled pairs to have fairly extensive rights within sections of the study area, the learning of prey sites and their rates of renewal may have been important components in their patterns of exploitation.'

Field studies such as these do tend to be somewhat artificial because they concentrate upon renewable resources in relatively simple, two-dimensional systems. Little attention has been given to other possible reasons for the observed drop in feeding rate which characterises an intruder.

Milinski and Heller (1978) found that when under high predation risk a stickleback's feeding behaviour changes and they suggested that the confusion effect and the need for vigilance under such conditions as a possible causal factor. Optimality models work on the theory that a feeding strategy adopted by an animal is the result of a trade off between costs and benefits to the animal's fitness. When predation risk is high, the fish suffers a cost, namely a lower rate of food intake but benefits from the greater awareness of a predator attack.

Thus the observed feeding behaviour is dependent upon the environmental pressures acting upon the animal. A feeding strategy which can be thought of as optimal under a certain set of environmental conditions may not prove to be so when those conditions change.

Pyke (1979) using data from Gill and Wolf (1975a) on the economics of territorial defence in sunbirds constructed four plausible optimality models for the behaviour and dispersion of the birds. He found that a strategy of minimising daily energetic cost had the best fit with the observed behaviour. The most important point that he made was that under different circumstances, one of the alternative hypotheses might be more appropriate. For instance, when the birds are storing up fat reserves for migration, a strategy of maximising net daily energy gain may be favoured.

In the same way sticklebacks may show different feeding strategies which are dependent upon environmental variables. The inclusion of a predator, Milinski and Heller (1978) showed, alters behaviour. I have shown that the resident/intruder effect has a similar outcome. An intruding male switches its feeding behaviour to allow for the presence of the resident male.

Cowie et al. (in prep, quoted in Krebs 1980) have tested the predator effect with captive Great Tits (*Parus major*). After exposure to a stuffed sparrowhawk (*Accipiter nisus*), hungry birds increased their frequency of looking up. Inter-prey waiting time and handling time also increased. It appears that when the birds assess the risk of predation to be high, fast feeding is compromised for greater vigilance, which supports their hypothesis that handling time is a trade off between vigilance and feeding.

The resident/intruder effect may have a profound influence upon the evolution of territorial systems in animals. Territorial defence is favoured by an even distribution of food supplies; animals partition out food resources as a result of territorial behaviour. Clearly the resident/intruder effect, once established will enhance territoriality as animals which persistently ignore territorial boundaries (if not detected and ousted by residents) will feed less successfully and thus tend on average to have a lower reproductive success. Within a territory, the owner will also need to be vigilant in order to detect an intrusion into its territory. However its feeding rate will not be as adversely affected as that of the intruder. The resident is likely, through knowledge of its territorial boundaries to know the best site on which to confront and displace the intruder. Once territoriality is established as a system, the resident/intruder effect sharpens up territorial boundaries. However once some form of spacing out has evolved, it is also possible to envisage that the resident/intruder component may enhance the evolution of territoriality.

SUMMARY

Recent studies (Davies and Houston 1981, Kamil 1978, Zach and Falls 1976b) have shown that intruders into territories feed less efficiently than residents. This is explained by the idea that residents are aware of the nature and location of the food supply within the territory - intruders are not. Whilst this would appear to be the case in the above mentioned studies I suggest that there is an extra component worthy of consideration. An intruders lower feeding rate and/or altered feeding behaviour may also be the result of a need for greater vigilance. Milinski and Heller (1978) have shown this to be the case when preadtion

pressure is high. The need for vigilance to detect the approach and possible attack of the resident similarly alters the feeding strategy of the intruder. The intruder must'keep an eye open'for the resident. Optimality models are determined by environmental variables. When one or more of these variables changes a new solution must be found to the trade off of costs and benefits to the animal's fitness.

REFERENCES

Allen (1920) The attacks of a loon _Garia immer_ upon a shoal of sardines _Sardinella coeruleus_ Starks and Morris. _Ecology_ _1_:309-310

Brown J.L. (1964) The evolution of diversity in avian territorial systems. _Wilson Bulletin_ _76_ (_2_): 160-169.

Brown J.L. and Orians G.H. (1970) Spacing patterns in mobile animals _A. Rev. Ecol. Syst._ _1_: 239-267.

Davies N.B. and Houston A.I. (1981) Owners and satellites: the economics of territory defence in the Pied Wagtail _Motacilla alba_ _Journal of Animal Ecology_ _50_ 157-180.

Krebs J.R. (1980) Optimal foraging and territorial defence. _Ardea_ _68_ 83-90.

Kamil A.C. (1978) Systematic foraging for nectar by Amakihi _Loxops virens_ _Journal of Comparative Physiology and Psychology_ _92_ 388-396

Milinski M. (1977a) Experiments on the selsection by predators against spatial oddity of their prey. _Z.Tierpsychol._ _43_ 311-325

Milinski M. (1977b) Do all members of a swarm suffer the same predation? _Z.Tierpsychol._ _45_ 373-388

Milinski M. and Heller R. (1978) The influence of a predator on the optimal foraging behaviour of sticklebacks _Gasterosteus aculeatus_. _Nature_:_275_ 642-644

Noble (1939) The role of dominabce in the social life of birds. _Auk_ 56 (3) 263-273.

Pyke G.H. (1979) The economics of Territory size and time budget in the Golden Winged Sunbird. _Amer. Nat._ _114_ 131-145

Rohwer (1978) Parent cannibalism of offspring and egg raiding as a Courtship strategy.in _Gasterosteus aculeatus_ _Amer.Nat._ 429-439.

Tinbergen N. (1951) The study of instinct Oxford.

Van den Assem J. (1967) Territory in the Three-spined stickleback *Gasterosteus aculeatus* - An experimental study in intra-specific competition. *Behaviour*. Supplement XVI.

Wilson E.O. (1971b) Competitive and aggressive behaviour. In J.F. Eisenberg and W.Dillon. eds. (qv.) *Man and Beast: Comparative Social Behaviour*. pp 183-217

Wilson E.O. (1975) *Sociobiology: The New Synthesis*. Belknap Harvard.

Zach and Falls (1976b) in *Canadian Journal of Zoology*.